Predicting the Ability of Marine Mammal Populations to Compensate for Behavioral Disturbances

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LONG-TERM GOALS

This project aims to develop new prospective analytical tools to determine the ability of marine mammal populations to compensate for behavioural disturbances. We aim for these tools to be generic and applicable in data-poor situations. To do so, we will extend on recent advances in behavioral ecological modelling in which behavioral strategies are defined using hierarchical models where behavior is a state emerging from a number of hidden processes. This hidden process is formalised as a system of linear equations in which motivations and condition influences behavior and behavior feeds back on motivation levels and condition. We focus on defining the state resilience of behavioral strategies by analyzing the transient dynamics of those behavioral strategies (system of linear equations). This will provide a framework to inform the propensity for population consequences to emerge from behavioral disturbances.

OBJECTIVES

- Develop measures to estimate the ability of marine mammal populations to compensate for behavioral disruptions.
- Determine whether behavioral constraints influence this behavioral resilience
- Use simulations to develop a framework to infer behavioral resilience in data poor conditions
- Test predictions from simulations using empirical data from a data-rich case study.

APPROACH

Measures of resilience and temporal predictability exist for a variety of data types[1]. The goal of this project is to introduce these measures to the study of animal behavior and use individual-based simulation, following models that have been developed for PCOD[2,7], to assess the role of behavioral predictability on behavioral resilience in different ecological and life history conditions.

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We can then assess the stability and state of this defined behavior system (a system of equations) over their parameter space in the same way that such measures have been estimated classically in systems of connected populations (e.g., predator-prey population dynamics).

Given a simple system of equations describing the feedback of foraging/traveling behaviour on hunger/fear motivations:

$$F_t = (1-\beta_F)F_{t-1} + \alpha_{hF}\cdot h_t - \alpha_{fF}\cdot f_t \qquad h_t = (1-\beta_h)h_{t-1} - \alpha_{Fh}\cdot F_{t-1} + \alpha_{Th}\cdot T_{t-1}$$
$$T_t = (1-\beta_T)T_{t-1} + \alpha_{fT}\cdot f_t - \alpha_{hT}\cdot h_t \qquad f_t = (1-\beta_f)f_{t-1} - \alpha_{Tf}\cdot T_{t-1} + \alpha_{Ff}\cdot F_{t-1}$$

where βs are the intrinsic rate of change for behaviors and motivations, and αs are the effect of behaviors on motivation and vice-versa, indicated by the subscripts (e.g. α_{Ff} is the effect of feeding on fear). In this system, if an animal is hungry it will be more likely to feed and once it feeds itself hunger will decrease. On the other hand, a particular behavior positively affects the motivation that drives another behavior, but is negatively affected by it. If an animal travels, its hunger will increase and it will become less likely to travel again.

We can linearize this system of equation and define its state and dynamics using its Jacobian matrix:

$$J = \begin{bmatrix} \frac{\partial F}{\partial F} & \frac{\partial F}{\partial h} & \frac{\partial F}{\partial T} & \frac{\partial F}{\partial f} \\ \frac{\partial h}{\partial F} & \frac{\partial h}{\partial h} & \frac{\partial h}{\partial T} & \frac{\partial h}{\partial f} \\ \frac{\partial T}{\partial F} & \frac{\partial T}{\partial h} & \frac{\partial T}{\partial T} & \frac{\partial T}{\partial f} \\ \frac{\partial f}{\partial F} & \frac{\partial f}{\partial h} & \frac{\partial f}{\partial T} & \frac{\partial f}{\partial f} \end{bmatrix}$$

The Jacobian matrix represents the best linear approximation of a differentiable function, or set of functions, near a given point. Hence the analysis of the Jacobian matrix of our dynamic system, with respect to its eigenvalues, determinant and trace, can give us its behavior near a stationary point.

The system's (engineering) resilience – speed of return to the positive equilibrium after a disturbance[3,4] – can be estimated as the maximum real absolute eigenvalue of the Jacobian matrix. Reactivity, the second measure of transient dynamics, describes the transient growth of perturbations away from the positive equilibrium. In other words, reactivity translates how much the system can be perturbed from equilibrium and points to its ecological resilience. It is defined as the maximal instantaneous rate at which perturbations can be amplified[3,4] and can be calculated as follows:

$$reactivity = \max\left\{\lambda_i((J + [J]^T)/2); \quad i = 1,\ldots,n\right\},$$

with λ_i being the eigenvalues of the Jacobian matrix, J.

The damping ratio of the system, the damping of the system's oscillations until stability is achieved, is estimated as the ratio of the first eigenvalue to the second eigenvalue. A low damping ratio suggests

that the system quickly stabilizes after a disturbance and may as well be indicative of high engineering resilience.

We will use bottom-up and top-down approaches to understand the relationship between resilience and behavioral predictability. Firstly, we will simulate perturbations and assess the level of perturbation required to tip the behavior system in another state. Secondly, we will simulate time series of behavior for individuals placed under different life history and ecological constraints and measure the resilience of their behavior system states.

States of behavior systems

We will use the same individual-based simulations[2,7] to assess the dynamics of behavior systems. Particularly, we will develop insights in the role of perturbations to change the state of the system. We will also assess whether the response to perturbation, that is the rate at which individuals return to their state after a perturbation, might change as the system approaches a tipping point[1]. This is important because it will provide a mean to rapidly assess the sensitivity of populations to perturbations in the wild. It will also inform how changes in behavior system states can impact vital rates.

Influence of life history strategies

Recent work on PCOD has developed some first insights in the differences that exist between capital and income breeders in their sensitivity to behavioral disturbances[5]. We will focus simulation work on testing how these two different life history tactics affect the resilience of the behavior system. We will assess the influence of ecological conditions by having individuals living in environments with different noise colors[6].

Influence of behavioral strategies

Recent studies show that northern elephant seals from Año Nuevo have three different foraging tactics at sea[7]. Some individuals use the Northeast Pacific, while others remain in coastal waters and others again use the North Pacific Transition Zone (NPTZ). Yet, these individuals come from the same colony and therefore have very similar constraints placed on their behavior. Such inter-individual variability can be interpreted as different states of the northern elephant seal's behavior system. Data on these different foraging strategies will be derived from an 8 year data set that is composed of measurements of over 300 adult female elephant seals. For these females the UCSC group has measured, foraging trip duration, foraging location (i.e. coastal vs NPTZ), mass gain over the trip, body composition over the trip, reproductive parameters (pregnant or not pregnant), and whether the pup survived. This provides a unique opportunity to estimate the resilience of these states and assess how disturbances can affect these multiple states. Importantly, we can also assess the consequences of disturbances in these three behavioral strategies by estimating how it affects changes in measured body conditions and pup survival[7]. Recent statistical modeling efforts provides the process model needed to simulate seal behavior and its consequences caused by alteration in mass gain. In addition, this model was fitted to the data available for the three behavioral strategies offering a unique opportunity to determine the stability and dynamics of each of the behavioral systems. We can then assess whether our interpretation of behavioral resilience match observed variation in pup survival under different natural perturbations for the three strategies.

We use the model developed by Schwick et al.[7] to define a system of behavioral equations in which two activities proxys (daily transit rate (T) and daily number of drift dives (V)) are influenced by lipid mass (L) and lipid mass gain is influenced by those two activities:

$$L_t = L_{t-1} + \alpha_0 - \alpha_1 T_t + \alpha_2 V_t - \alpha_3 \frac{L_{t-1}}{R_{t-1}}$$

$$T_t = \beta_0 + \beta_1 \frac{L_t}{R_t} - \beta_2 V_t$$

$$V_t = \gamma_0 - \gamma_1 \frac{L_t}{R_t} - \gamma_2 T_t$$

where $\frac{L_t}{R_t}$ is the lipid to lean mass ratio on day t and R_t is estimated as linearly increasing between two observed measures of R: R_0, lean mass when leaving the colony and R_T, lean mass when returning to the colony[7]. Hence, $\frac{dR}{dt} = r$ a constant daily increased that is estimated from observations.

The Jacobian of this system is

$$J = \begin{bmatrix} 1 - \frac{\alpha_3}{r} & -\alpha_1 & \alpha_2 \\ \frac{\beta_1}{r} & 0 & -\beta_2 \\ \frac{-\gamma_1}{r} & -\gamma_2 & 0 \end{bmatrix}$$

Since the time series of daily lipid mass gain were previously estimated from observations[7] we can therefore fit the system of equations described above to the data (daily lipid mass gain, daily transit rate, and daily number of drift dives) using linear models to estimate the eight parameters in J in order to estimate the stability and resilience of each behavioral strategies.

We can then use ancillary data to assess whether our inferred resilience indeed matches the resilience observed under natural perturbations.

WORK COMPLETED

We have now developed simulations of a two behavior (foraging/travelling) -two motivations (hunger/fear) system of linear equations and explored a range of resilience measures to determine which may be most suited to represent the ability to compensate for behavioral disruptions. This work showed that both measures of transient dynamics, reactivity and resilience, represent different aspects of resilience and cannot be taken in isolation to define the behavior of the system around its stationary point. These will be the measures we will use to estimate the ability of marine mammal populations to compensate. We will therefore simulate behavioral time series to have a range of both measures and will estimate both measures for the northern elephant seals study. This work is now a manuscript (Barros & Lusseau 2013) due to be submitted to PLoS Computational Biology in October 2013.

RESULTS

Our preliminary simulation work help to highlight that two measures of resilience (reactivity and engineering resilience) will be necessary to capture the full transient dynamics of behavioral systems after perturbations.

We have now a workplan for the next 12 months. We anticipate the postdoctoral fellow (PDRF) to be in place in November 2013. The post has been advertised.

- Nov-Feb: adapt agent-based simulation platform[2] to assess the effects of behavioral constraints on resilience (life history characteristics and varying environmental noise)
- Feb: David Lusseau (PI1) and PDRF visit to UCSC to discuss plan with Dan Costa (PI2) for analysing the northern elephant seal's behavioral strategies, visit the field site and determine ancillary variable collected on individuals that can be used to determine whether strategies are resilient to perturbations.
- Mar-May: implement elephant seal models
- June-July: determine variability in rate of recovery from perturbation as system approaches tipping point between two stationary solutions using both empirical data from elephant seal case study and simulations.
- Aug: presentation of the elephant seal case study at ESA 2013.
- Aug-Oct: Use simulations to develop a framework to infer behavioral resilience in data poor conditions. We will test sampling requirement for robust estimation of resilience and reactivitity statistics, focussing on behavioural predictability as a proxy for resilience.

We anticipate three further publications in addition to Barros & Lusseau 2013.

IMPACT/APPLICATIONS

We will address needs to assess population consequences of acoustic disturbance (PCAD using PCOD framework) and provide a modeling framework for environmental compliance. We will develop means to assess the abilities of marine mammal populations to compensate for behavioral disturbances. This will provide a framework to inform the propensity for population consequences to emerge from behavioral disturbances, particularly in data poor conditions. In addition, this work will provide new metrics to complement efforts to implement PCOD in situations where data availability is limited.

RELATED PROJECTS

None.

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PUBLICATIONS

Barros C. & Lusseau D. 2013. Behavioural resilience and stability is influenced by motivational feedback rate. PLoS Computational Biology [to be submitted, refereed]